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STRUCTURE AND COMPOSITION OF SUBALPINE CONIFERS IN THE EMERALD LAKE WATERSHED, SEQUOIA NATIONAL PARK, CALIFORNIA

PHILIP W. RUNDEL
Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095
rundel@biology.ucla.edu

ABSTRACT

The Emerald Lake watershed forms a subalpine basin in the upper drainage of the Marble Fork of the Kaweah River in Sequoia National Park, California, with elevations ranging from 2804–3416 m. Five conifer species are present in the basin, with western white pine (*Pinus monticola* Douglas ex D. Don) as the most dominant species forming 71% of the stems and 82% of basal area censused in 1985 and 1986. Lodgepole pine (*Pinus contorta* Loudon subsp. *murrayana* (Grev. & Balf.) Critchf.) was the second most dominant in the watershed as measured by numbers of individuals and basal area, but was almost entirely restricted to mesic bench and wet meadow habitats in the lower elevations of the watershed. Foxtail pine (*Pinus balfouriana* Grev. & Balf.) comprised 9.5% of the stems and 13.7% of the basal area within the basin, but was largely present on higher north-facing ridgelines where it formed 52% of stems and 65% of basal area. Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), and red fir (*Abies magnifica* A. Murray bis var. *critchfieldii* Lanner) were present in small numbers in the lower basin in wet meadow and/or mesic granite bench habitats.

Key Words: Emerald Lake, *Pinus balfouriana, Pinus contorta* subsp. *murrayana, Pinus jeffreyi, Pinus monticola,* Sequoia National Park, subalpine conifer, treeline.

Subalpine and alpine basins of the Sierra Nevada provide significant ecosystems not only for their biodiversity, but also for monitoring environmental impacts of global change including higher temperatures, altered patterns of snowmelt, and the deposition of anthropogenic nitrogen and phosphorus (Millar and Rundel 2016). These high mountain ecosystems are sensitive to small changes in growing season conditions of temperature and water availability, and their stability impacts hydrological conditions which provide a critical resource for downstream agriculture and urban development in California (Bales et al. 2006; Maurer 2007; Trujillo et al. 2012). Of particular concern, therefore, is the potential for alterations of the hydrology and thermal conditions in the Sierra Nevada that may impact the length of growing seasons and water availability and through such changes the community structure and productivity of high mountain ecosystems. Such changes may already be occurring. Data from vertebrate studies have indicated significant upward elevational range shifts for a number of species of birds and mammals over the past century (Moritz et al. 2008; Tingley et al. 2009), and subalpine plant species are expected to respond in a similar manner (Millar and Rundel 2016). Subalpine conifers, which form the major part of the basin biomass, represent a critical element for the stability of community and food web structure (Millar and Rundel 2016).

Studies of forest demography in the Sierra Nevada, as well as across the western United States, have reported an increase in overall mortality rate over recent decades in species of both *Pinus* and *Abies* (van Mantgem and Stephenson 2007; van Mantgem et al. 2009). However, the magnitude of changes in mortality rate declined with increasing elevation, and there was no significant increase in mortality in subalpine plots (van Mantgem and Stephenson 2007). Concern about patterns of increasing mortality led Stephenson and van Mantgem (2005) to point out the need for increased baseline sampling efforts to definitively detect changes at high elevations.

The constrained size of the Emerald Lake watershed provided an opportunity for a detailed demographic survey of the size distribution and habitat of subalpine conifers. The objective of these data, when first collected decades ago, was to provide a complete census and measurement of every individual tree growing within the watershed and to categorize tree population and community structure within the physiographic habitats of the watershed. In addition, samples were collected to quantify branch tip growth and needle retention, covering a 5-yr period predating the study as a measure of interannual changes in growth conditions for the three important pine species. These data thus provide a rich baseline source of information for future studies.

METHODS

Study Site

The Emerald Lake watershed in Sequoia National Park has served for more than three decades as a

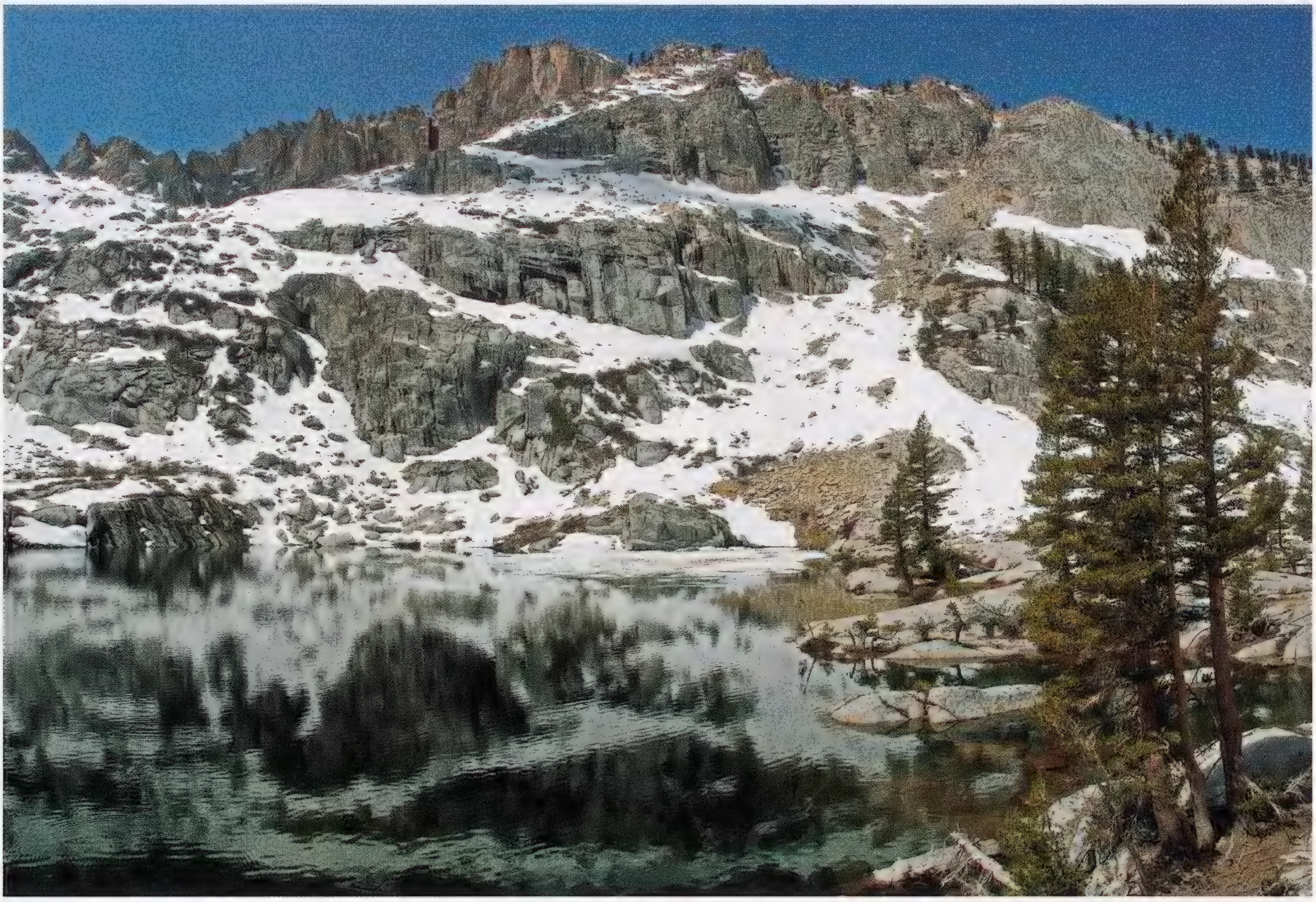

FIG. 1. Emerald Lake Basin, Sequoia National Park, with Emerald Lake (2804 m) in the foreground and looking up to Alta Peak (3415 m). National Park Service photo by Rick Cain.

primary study site to understand the hydrology, ecology, and biogeochemistry of a representative subalpine basin in the southern Sierra Nevada (Fig. 1). The watershed, 120 ha in area, covers an elevational range from 2804 m at Emerald Lake to 3416 m at the summit of Alta Peak (Fig. 2). The Emerald Lake Basin is a glacial cirque, carved from granitic parent material and representative of many subalpine and alpine basins in the Sierra Nevada with lakes exhibiting weakly buffered calcium bicarbonate surface waters (Williams and Melack 1991). The climate of the Emerald Lake watershed is typical of the Mediterranean-type regime of the southern Sierra Nevada, with 75–90% the annual precipitation falling as snow in the winter months (Stephenson 1988). Based on limited long-term data on precipitation levels, mean annual precipitation is about 1600 mm, but amounts are highly variable between years (Sickman et al. 2003a). Snowmelt typically begins in April with peak flow of runoff water occurring in June (Sickman et al. 2003b). Summers are generally dry except for an occasional convective storm associated with monsoonal air masses from the east (Sadro and Melack 2012).

Bedrock exposed by glacial scouring and frost action covers nearly half of the surface area of the Emerald Lake watershed, with the remaining half covered by talus and thin soils in approximately equal proportions, with soils present over only about 20% of the watershed surface (Sisson and Moore 1984; Tonnessen 1991), vascular plant cover is relatively sparse. Thin soils and fractures in the granite surface, however, do support a wide distribution of both wet and dry meadow communities throughout the basin. Furthermore, extensive woody shrub growth in local areas of the lower basin appear where soils are more developed and in rocky fracture lines across the basin where soil and moisture are available. Because of the rocky nature of the watershed, plant cover is highly restricted, although there are open stands of subalpine conifers as well as willow thickets (Rundel 2015), wet and dry meadows, and scattered plant growth in rock crevices, fellfields, and areas of colluvium. The flora is surprisingly large considering the limited area of developed soil profiles, with 202 vascular plant species present (Rundel et al. 2009).

Intensive research on hydrology and biogeochemical cycling in the Emerald Lake watershed began in 1984, with funding from the California Air Resources Board, to address concerns related to the influence of atmospheric inputs of nutrients to basin processes and ecosystem structure (Tonnessen 1991). Watershed ecosystem studies at this site have continued up to the present day and have provided detailed (and in many cases) long-term and continuing databases to

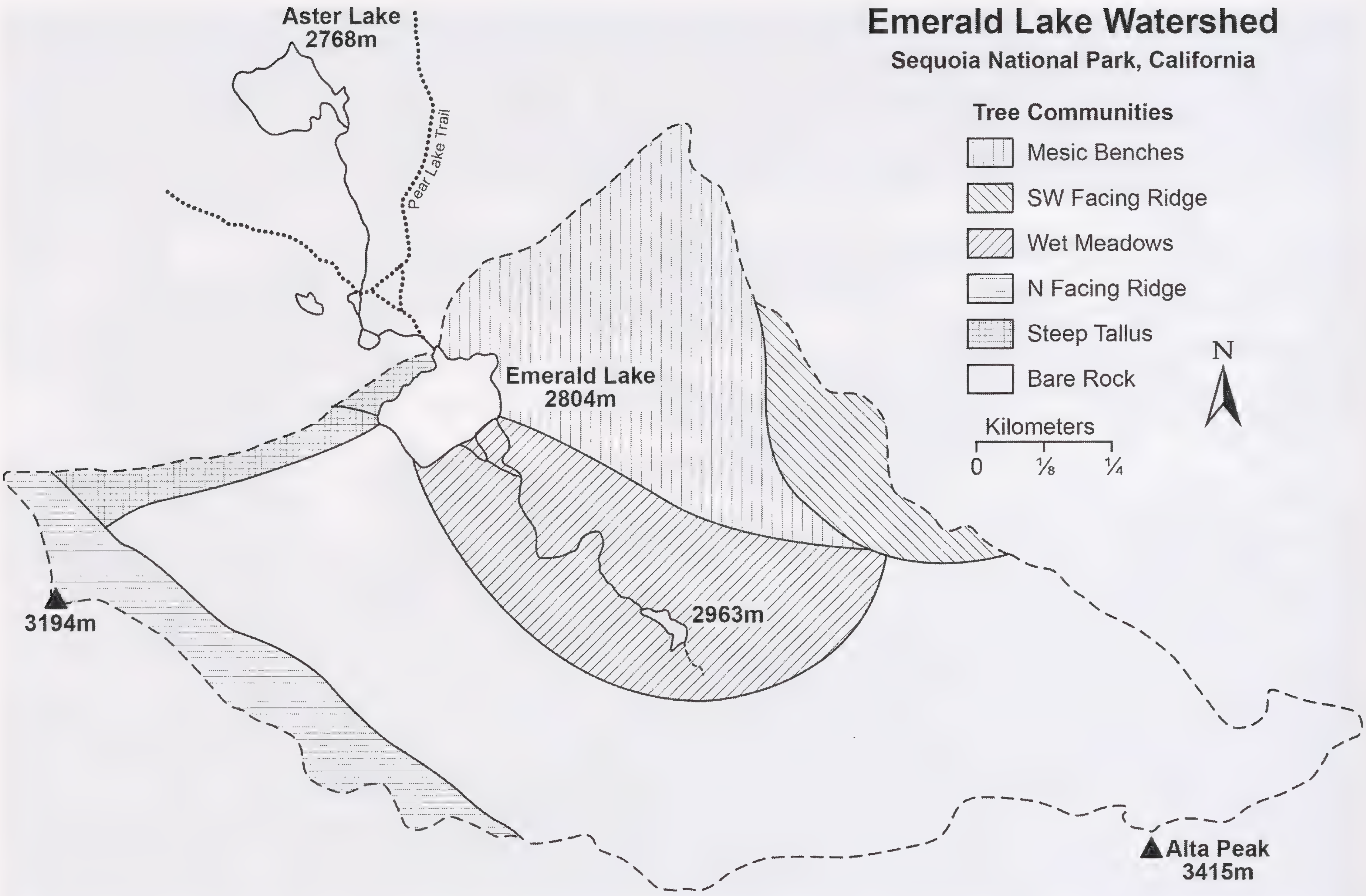

FIG. 2. Map of the Emerald Lake watershed showing the major physiographic divisions.

understand hydrologic flow and water balance (Kattelmann and Elder 1991; Huth et al. 2004), nutrient enrichment (Sickman et al. 2003a, b), solute chemistry of snowmelt and runoff (Williams and Melack 1991), nitrogen fluxes and transformations (Miller et al. 2009), and models of hydrochemical response (Wolford et al. 1996; Wolford and Bales 1996; Meixner et al. 2004).

Field Measurements

A complete field census of all trees in the Emerald Lake watershed was carried out over the summers of 1985 and 1986. Each tree was identified, measured for diameter at breast height (dbh) to the nearest 1 cm. For saplings that did not reach breast height, the diameter measured was that of the stem base. No seedlings or small saplings of any species were found with basal diameters <5 cm. Stems were roughly mapped within each of five physiographic community habitats identified within the watershed. Habitats were determined by a combination of criteria, including physiographic position, substrate, moisture availability, exposure, and community composition, that together defined distinct assemblages. These habitats were mesic bench, wet meadow, southwest-facing ridgeline, north-facing ridgeline, and steep talus slopes. A major portion of the watershed area was bare rock without individual tree stems. The relationship between dbh and height was measured in 65 stems of *Pinus monticola* Douglas ex D. Don growing in permanent plots established in the wet meadow and mesic bench habitats.

Phenological patterns of vegetative and reproductive growth were followed over four growing seasons to provide a measure of interannual variation in growth characteristics for three pine species. In October and November 1986, 20 actively growing branches collected from five individuals each of *Pinus balfouriana* Grev. & Balf., *P. contorta* subsp. *murrayana,* and *P. monticola* were harvested to provide quantitative data on the relative growth of branch tip elongation and biomass over the past five growing seasons. Measures of needle length, twig length, and biomass per growing branch tip were made for the years 1982–1986. Numbers of living needle fascicles and fascicle scars were counted for the past five growing seasons to evaluate needle retention over five growing seasons.

RESULTS

Tree Distribution and Composition

The conifer community of the Emerald Lake Basin included 1206 stems with five species present in the 120 ha area of the watershed. These were *Pinus monticola* (western white pine), *P. contorta* subsp. *murrayana* (lodgepole pine), *P. balfouriana* (foxtail pine), *P. jeffreyi* Grev. & Balf (Jeffrey pine), and A. Murray bis *magnifica* var. *crichfieldii* Lanner (red fir).

TABLE 1. Total tree density and basal area within each of the major physiographic habitats of the Emerald Lake watershed. Relative values in percent for the entire watershed are shown in parentheses.

	Area (ha^2)	Stems	Stem density (no. ha^{-1})	Basal area (m^2)	Basal area density (m^2 ha^{-1})
Bare rock	59.6 (49.7%)	0	0.0	0	0.0
Mesic bench	23.5 (19.6%)	581 (48.2%)	24.7	89.0 (51.1%)	4.2
SW-facing ridge	8.9 (7.4%)	300 (24.9%)	33.8	44.3 (25.4%)	7.9
Wet meadow	19.1 (15.9%)	100 (8.3%)	5.2	5.9 (3.4%)	0.3
Steep talus	3.2 (2.7%)	57 (4.7%)	17.6	1.7 (1.0%)	0.5
N-facing ridge	5.6 (4.7%)	168 (13.9%)	29.8	33.3 (19.1%)	3.7
Total watershed	120 (100)	1206 (100)	10.1	174.2 (100)	1.45

The conifer community has a mean density of 10.1 trees ha^{-1} for the entire watershed. On a basal area basis, the watershed contained 174.5 m^2 of tree basal area, or 1.45 m^2 ha^{-1}. These figures on density and basal area are misleading as more than half of the watershed is treeless and covered by bare granite outcrops (Fig. 1).

Breaking down the watershed's conifer community by slope exposure, 73.1% of trees were located on southwest-facing exposures. Northwest and north facing exposures contained 8.3% and 18.7%, respectively, of the basin trees. These values were close to the relative basal area present on each of these three exposures (Table 1). West facing exposures below Alta peak were smooth granite outcrops presenting little to no available habitat for tree establishment, while the orientation of the basin provide few areas with east-facing exposure.

The most abundant tree species in the watershed was western white pine with 71.2% (859 trees) of the total conifer community (Table 2). Next in abundance were lodgepole pine with 16.7% (202 trees) and foxtail pine with 9.5% (114 trees) in the basin. Only small numbers of red fir (20 trees) and Jeffrey pine (11 trees) were present. The distribution of relative basal area among the five conifers generally followed the relative density, but with increased relative dominance by western white pine (82.4%) and foxtail pine (13.7%).

The distribution of stems of western white pine by size-class displayed a typical inverse J-shape distribution with many smaller trees and relatively few large trees (Fig. 3A). Nearly 60% of the stems had a dbh of 15 cm or less. However, there seemed to be a secondary small peak of tree abundance for stems above 50 cm dbh, suggesting lower rates of mortality for these larger and hypothetically older trees. Some caution must be used in this interpretation since size is not a strong correlate of age in subalpine conifers (LaMarche and Mooney 1972; Brunstein and Yamaguchi 1992). Despite the high elevation and rocky substrate of the watershed, western white pine stems reached diameters up to 195 cm, with 70 trees with dbh >100 cm. All but nine of these occurred on the mesic bench habitat, with six on the north-facing ridge and three in the wet meadow area.

Lodgepole pine also exhibited an inverse J-shape distribution of size-class with many small trees and only very few stems reaching dbh of 50 cm or more (Fig. 3B). More than 60% of the stems were in the 15 cm or smaller dbh class. There were four trees over 50 cm over in diameter, with the largest individual in the watershed having a dbh of 97 cm.

The size-class distribution of foxtail pine in the watershed was heavily weighted toward stems of larger size compared with western white pine (Fig. 3C). There were proportionally fewer stems in the

TABLE 2. Distribution of trees and tree basal area within the entire Emerald Lake watershed and within each of the five physiographic habitats. Relative values in percent for each habitat are shown in parentheses.

	P. monticola	*P. contorta*	*P. balfouriana*	*P. magnifica*	*P. jeffreyi*	Total
Frequency (stems)						
Total watershed	859 (71.2%)	202 (16.7%)	114 (9.5)	20 (1.7%)	11 (0.9%)	1206
Mesic bench	419 (72.1%)	138 (23.8%)	0	13 (2.2%)	11 (1.9%)	581
SW-facing ridge	238 (79.3%)	36 (12.0%)	19 (6.3)	7 (2.3%)	0	300
N-facing ridge	77 (45.8%)	3 (1.8%)	88 (52.4)	0	0	168
Wet meadow	72 (72.0%)	23 (23.0%)	5 (5.0)	0	0	100
Steep talus	53 (93.0%)	2 (3.5%)	2 (3.5)	0	0	57
Basal area (m^2)						
Total watershed	143.8 (82.4%)	6.1 (3.5%)	23.9 (13.7%)	0.7 (0.4%)	0.7 (0.4%)	174.5
Mesic bench	83.4 (93.7%)	5.1 (5.7%)	0	0.4 (0.6%)	0.1 (<0.1%)	89.0
SW-facing ridge	43.3 (94.0%)	0.6 (1.4%)	2.1 (4.5%)	0.1 (0.1%)	0	46.1
N-facing ridge	11.5 (34.6%)	0.1 (0.2%)	21.7 (65.1%)	0	0	33.3
Wet meadow	5.2 (91.4%)	0.4 (6.5%)	0.2 (2.1%)	0	0	5.9
Steep talus	1.6 (93%)	0.06 (3.5%)	0.06 (3.5%)	0	0	0.2

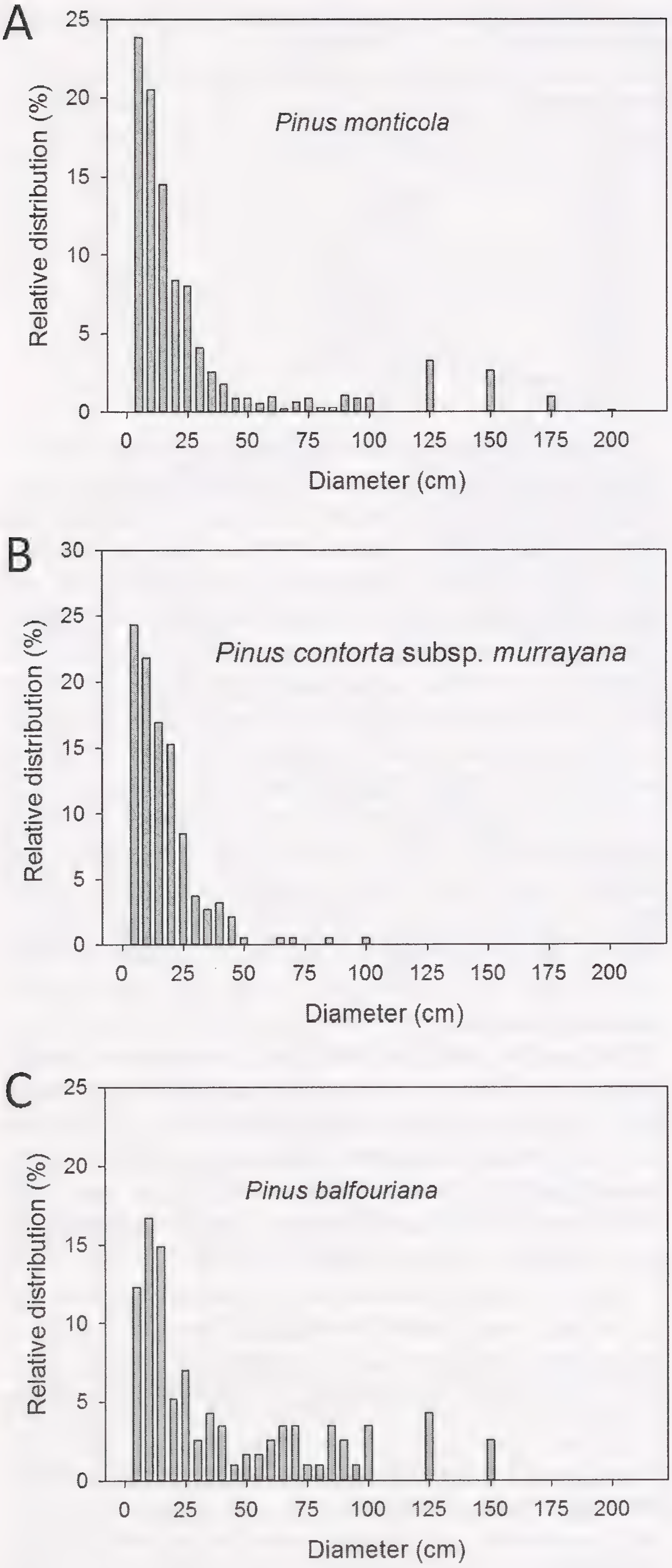

FIG. 3. Relative distribution by diameter class for *Pinus balfouriana*, *P. contorta* subsp. *murrayana*, and *P. monticola* in the Emerald Lake watershed. Large trees were measured to their dbh in cm and plotted here into their 5 cm class of diameters.

smaller dbh classes of <15 cm, although reproduction was taking place as these comprised over 40% of all stems. There were six trees that reached a dbh >100 cm, with the largest tree having a dbh =146 cm.

Jeffrey pine was only represented by 11 stems, all of these growing at lower elevations in the mesic bench habitat. All of these had a dbh of 15 cm or less. Red fir was also rare in the watershed, represented by just 20 stems with two-thirds of these growing in the mesic bench habitat. Three-quarters of the stems were in the small dbh classes of 15 cm or less, but there were three stems that had diameters of 31–47 cm, all in the mesic bench habitat, which likely represent an earlier period of establishment.

To assess patterns of tree distribution within the watershed beyond simple slope exposure, the Emerald Lake watershed was categorized into six physiographic habitats (Fig. 2). Approximately 60% of the watershed area, including all of the steep slopes below Alta Peak, was bare granite outcrops that lacked trees. The largest habitat type supporting trees was formed by mesic rock benches extending from Emerald Lake itself southeast along several input streams to about 3000 m elevation. These covered 19.6 ha (23.5%) of the basin. Wet meadow habitats spread across the north central area of the watershed at lower elevations covered 19.1 ha, (15.9%) of the area. The southwest-facing ridgeline along portions of the eastern boundary of the watershed covered 8.9 ha (7.4%) of the basin. The north-facing ridgeline along much of the upper southwestern boundary of the watershed covered 5.6 ha (4.7%) of the basin, while steep talus slopes along the northwest margin of the basin covered 3.2 ha (2.7%) of the watershed.

Breaking tree distribution down by habitat type, 48.2% (581 trees) were located in the mesic bench area of the watershed (Table 1). These accounted for 51.1% (89 m^2) of the total basal area of trees in the watershed. For this habitat, mean tree density was 24.7 trees ha^{-1} with a mean basal area of 4.2 m^2 ha^{-1}. Western white pine was the dominant species but nearly one quarter of trees present were lodgepole pine. This habitat at lower elevations and milder conditions within the watershed was home to two-thirds of the red fir and all of the Jeffrey pine. By contrast, there were no foxtail pines in this habitat.

Next in importance for tree distribution among the habitats was the southwest-facing ridge community, which despite its relatively small area included 24.9% (300 trees) of watershed stems and 25.4% (44.3 m^2) of watershed basal area. Mean tree density was 33.8 trees ha^{-1} with a mean basal area of 7.9 m^2 ha^{-1}. This habitat was dominated by western white pine, which made up 79.3% of stems and 93.8% of basal area.

The north facing ridgeline was home to 13.9% (168 trees) of watershed stems, with 19.1% (33.3 m^2) of watershed basal area. Mean tree density was 29.8 trees ha^{-1} with a mean basal area of 3.7 m^2 ha^{-1}. This was the favored habitat of foxtail pine in the basin with almost 89% of all of the foxtail pines occurring on this north-facing ridgeline. This species accounts for 52.4% of stems and 65% of the basal area for this habitat, with western white pine making up almost all of the remaining basal area.

The wet meadow habitat included 8.3% (100 trees) of watershed stems, with 3.4% (5.7 m^2) of watershed basal area. Mean tree density was 5.2 trees ha^{-1}, with

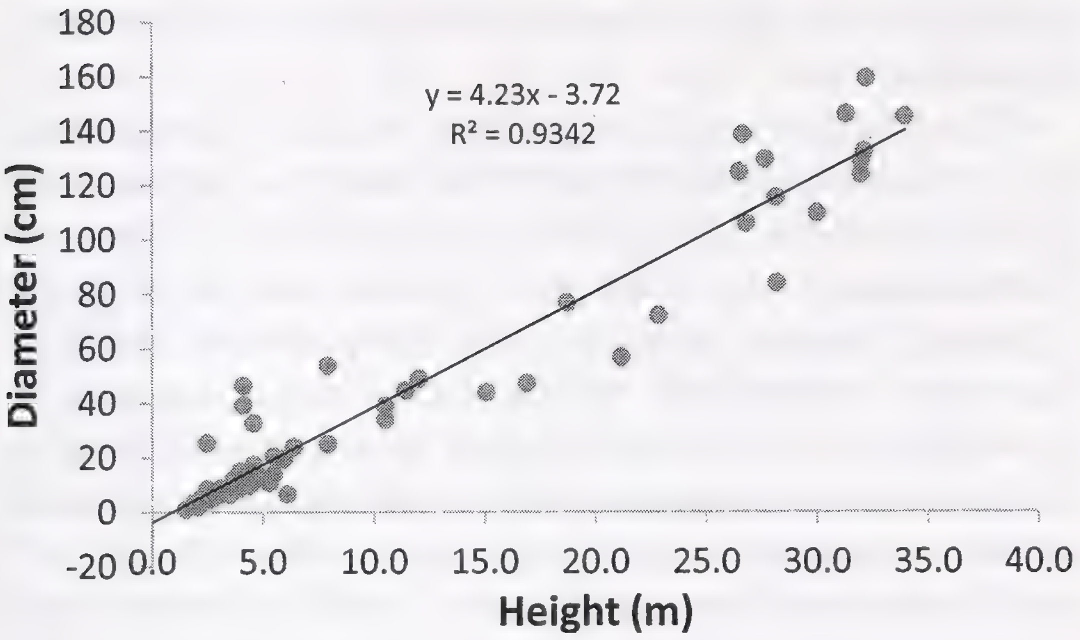

FIG. 4. Relationship of diameter at breast height to height of *Pinus monticola* growing in wet meadow and mesic bench habitats in the Emerald Lake watershed (n = 65).

a mean basal area of 0.3 m^2 ha^{-1}. The conifer community here was dominated by western white pine, with a significant presence of lodgepole pine.

The steep talus slopes, the smallest of the habitat areas, was home to only 4.7% (57 trees) of the watershed trees, and 1.0% (1.7 m^2) of basal area. Mean tree density, however, was 17.6 trees ha^{-1} but with only a mean basal area of 0.5 m^2 ha^{-1} because of small tree sizes. Almost all of the trees on these slopes were western white pine.

Diameter at breast height showed a linear relationship to tree height in western white pine (Fig. 4). Seven trees in those sampled had heights >30 m, with the tallest reaching 34 m. Several trees with intermediate diameters of 40–80 cm had heights well below that predicted for a regression, reflecting a combination of poor growing sites in granite cracks or past lightning strikes.

Tree Growth Rates and Needle Retention

The timing of the phenological events of new needle initiation, needle maturity, and branch elongation of growing tips varied among years for lodgepole pine and western white pine. Juvenile needles began to form in late May and continued to expand until early August. Branch elongation was apparent in up to 50% of trees by late June and was completed by early August, reflecting a short growing season in this habitat. Preformed buds for the following growing season were visible beginning in early to late August depending on the year. Mean needle length, annual twig growth, and biomass per annual growth node showed variation, but no consistent pattern over the 5 yr of study for the three dominant pine species (Table 3).

TABLE 4. Relative needle retention for 5 yr in *Pinus balfouriana*, *P. contorta* subsp. *murrayana*, and *P. monticola* in the Emerald Lake watershed. Values shown are percent needle retention at the end of each growing season from the cohort of needles formed in 1982.

Year	*P. balfouriana*	*P. contorta*	*P. monticola*
1 (1982)	100	98	100
2 (1983)	91	95	91
3 (1984)	83	81	83
4 (1985)	80	79	68
5 (1986)	64	67	42

Relative needle retention over the 5 yr of study was very similar in the three dominant in species, with over 81–83% retention of first growing season cohorts of needles at the end of the third growing season (Table 4). By the end of five growing seasons, western white pine retained only 40% of its of 1982 growing season cohorts of needles, while foxtail pine and lodgepole pine retained close to 64%–67%, respectively.

DISCUSSION

Subalpine stands of conifers in the Emerald Lake watershed are representative of those in other parts of the central and southern Sierra Nevada (Millar and Rundel 2016). Western white pine, the dominant species at Emerald Lake, is locally abundant in subalpine habitats along the western slope of the Sierra Nevada, where it may occur in small pure stands but more commonly is found mixed with lodgepole pine, Jeffrey pine, mountain hemlock, and red fir (Potter 1998). Although trees of this species may reach 40 m in height and 2.5 m in diameter in the Sierra Nevada, these sizes are smaller than those reached by western white pines in the northern Rocky Mountains and Pacific Northwest (Van Pelt 2001). Western white pine generally maintains a tree form of growth up nearly to treeline, where it is commonly replaced in the Sierra Nevada by white-

TABLE 3. Five-year record of mean needle length, twig length for new growth, and biomass per growing tip for *Pinus balfouriana* (PIBA), *Pinus contorta* subsp. *murrayana* (PICO), and *Pinus monticola* (PIMO) in the Emerald Lake watershed, Sequoia National Park. Field samples were collected in October and November 1986. Standard deviations of mean values for measurements of 20 branches collected from five trees are shown in parentheses.

	Needle length (mm)			Twig length (mm)			Biomass / node (mg)		
	PIBA	PICO	PIMO	PIBA	PICO	PIMO	PIBA	PICO	PIMO
1986	24 (5)	33 (7)	41 (6)	13.8 (6.2)	21.6 (7.0)	22.2 (9.4)	799 (539)	1090 (418)	970 (328)
1985	25 (4)	46 (8)	49 (4)	16.9 (6.1)	30.4 (9.8)	25.9 (8.5)	962 (546)	2271 (742)	1428 (399)
1984	25 (4)	39 (6)	47 (5)	14.1 (5.1)	20.6 (4.1)	21.1 (8.6)	929 (429)	1463 (380)	1087 (300)
1983	18 (5)	25 (6)	30 (8)	12.1 (5.0)	20.6 (5.2)	19.4 (7.0)	744 (640)	937 (386)	698 (236)
1982	21 (5)	33 (9)	41 (5)	12.3 (4.1)	21.0 (5.4)	21.6 (11.1)	717 (507)	1217 (461)	885 (359)

bark pine or foxtail pine on rocky ridges (Millar and Rundel 2016). Western white pine seedlings are reported to be relatively rare compared to other subalpine conifers (Parker 1988).

Open stands of lodgepole pine forests make up a widespread upper montane forest/woodland over much of the species' range, tolerating both shallow rocky soils and semi-saturated meadow edges, in an elevational belt both within and above the red fir zone (Potter 1998; Fites-Kaufman et al. 2007). These open forests generally occur at elevations of about 1,830–2,400 m in the northern Sierra Nevada, and rise to 2440–3350 m in the south. Thus, the Emerald Lake basin lies near the upper elevational limits of this species. Topography has a strong influence on elevational distribution, and lodgepole pine forests may reach into much lower elevations with cold air drainage down glacial canyons (Potter 1998; Fites-Kaufman et al. 2007).

Foxtail pine is the dominant treeline pine in the southern Sierra Nevada, where it is restricted to higher elevations of 2,600–3,660 m south of the Middle Fork of the Kings River. At its lower elevational limits, this species may occur in open stands with lodgepole pine, Jeffrey pine, western white pine, and red fir (Millar and Rundel 2016). At higher elevations, however, it forms relatively pure, but low density stands. It has been suggested that foxtail pine populations in the southern Sierra Nevada likely persisted through the Pleistocene in ice-free ridgetop habitats (Eckert et al. 2008). Field studies have suggested that soil moisture availability is the most critical variable for determining fine-scale patterns of growth (Bunn et al. 2005).

Vankat and Major (1978) sampled stands of foxtail pine from elevations of 3170–3290 m in Sequoia National Park and reported a relatively high mean density of 418 tree ha^{-1}, with a canopy cover of 26%, and a basal area of 31 m^2 ha^{-1}. The present study found much lower densities, but higher basal area. Tree densities and stand basal areas decline with increasing elevation from foxtail pine woodlands to treeline (Lloyd 1997). Foxtail pines have great longevity and can grow to be several thousand years old (Millar and Rundel 2016). Like bristlecone pine, foxtail pine has wood that is highly resinous, and, combined with cold, arid climates in the southern Sierra Nevada, remnant dead wood can persist for millennia. Together the live and dead wood are important archives for paleoclimatic and paleoecologic study, and foxtail pines have been documented to respond to warm and cold historic climate periods by, respectively, advancing upslope and retracting downslope (Scuderi 1993; Lloyd and Graumlich 1997; Millar et al. 2004).

Jeffrey pine commonly occurs on rocky or more arid slopes at elevations of 1600–2600 m in the southern Sierra Nevada (Millar and Rundel 2016), but reaches to 3000 m or more in favorable sites as at Emerald Lake. Similarly, the small population of red fir at Emerald Lake occurs near the upper elevation limit of this species and is restricted to the most favorable sites.

The results from elongation rates of pine branch tips as a surrogate for growth conditions suggest that interannual variation in these conditions have not been dramatically different over the period of years sampled. Increasing impacts of air pollution on high elevation watersheds in California were one of the concerns that led to the broad program of Emerald Lake studies (Tonnessen 1991). Shortened periods of needle retention, a measure associated with oxidant air pollution (Arbaugh et al. 2003), were not apparent in the current study.

Historical studies of the growth dynamics of subalpine trees in the Sierra Nevada have highlighted the complexity of responses to cyclic interactions between temperature and moisture at a regional level (Millar et al. 2004; Millar and Rundel 2016). Spatial tree patterns in these ecosystems (exemplified here by the Emerald Lake watershed) respond directionally to century-long climate trends, and may exhibit abrupt and reversible effects as a consequence of multi-decadal climate variability. Significant interactions among temperature, multiyear variability in moisture availability, and the Pacific Decadal Oscillation are all interrelated factors, with ecological responses driven in particular by minimum temperatures and their impact on snowmelt (Millar and Rundel 2016). Thus, global change may well have very strong impacts on the structure of subalpine tree communities, although with some expected lag time in these long-lived species. The detailed population structure of conifers collected three decades ago in the Emerald Lake watershed may serve as a basis for interpreting possible future changes in stand structure and growth rates.

There is growing evidence that rates of warming are elevation-dependent and that higher elevations are changing faster than lower elevations, perhaps due to increased sensitivity to forcing factors (Diaz and Bradley 1997). If this is the case, and exceptional growth rates for subalpine species (e.g., bristlecone pine in the White Mountains, Salzer et al. 2009), suggest that it is, then subalpine forests might well face rates of warming faster than projected for the California lowlands. Temperature may no longer be the main limiting factor for growth of bristlecone pine on south-facing slopes near treeline in the White Mountains, suggesting that increasing warmth may lead to a divergence between tree growth and temperature at previously temperature-limited sites (Salzer et al. 2014).

Mountains have enormous heterogeneity in slope, aspect, topography, regional context, and landform, as seen in the distinct, but separate, community assemblages of conifers within the Emerald Lake watershed. This patchiness translates to complexity in meso- and micro-climatic variation (Daly et al. 2007; Lundquist and Cayan 2007; Graham et al. 2012), potentially providing subalpine and alpine plants and animals with potential favorable escape opportunities other than simple migration upslope. An example of this can be seen where cold-air drainage creates positive lapse rate conditions (i.e., decreasing temperature with declining elevation) in montane environments There are hints that this process might actually increase in the future under forcing factors of anthropogenic climate change (Pepin and Lundquist 2008), resulting in the net effect that canyon bottoms, basins, and swales may become cooler than slopes and summits. In addition, diverse microclimates relatively independent of elevation may occur as with special geomorphic features, such as rock glaciers, buffer local conditions of temperature and moisture availability (Millar and Rundel 2016; Millar et al. 2016).

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